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SOME MIDDLE DEVONIAN (EIFELIAN-GIVETIAN) FOSSIL FISH REMAINS FROM THE PIMENTEIRA FORMATION OF THE PARNAÍBA BASIN, NORTHEAST BRAZIL [1]

(With 4 figures)

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ABSTRACT: Some Middle Devonian (late Eifelian-early Givetian) fossil fish remains are described from an outcrop of the Pimenteira Formation on the eastern border of the Parnaíba Basin (Picos area, State of Piauí, northeast Brazil). These remains include a fin spine with ribbed ornament, a bicuspid shark tooth similar to those of xenacanths and omalodontids, a badly-preserved *Machaeracanthus* spine, and small indeterminate scales and fragments of what may be prismatically calcified cartilage. The bicuspid tooth is the first record of its kind from the Devonian of Brazil and the first unequivocal Devonian record from South America. Its principal cusps have widely spaced cristae, like teeth of the Gondwanan Devonian elasmobranch *Antarctilamna*, but small intermediate cusps are absent (as in *Leonodus*). The fin spine has comparable ornament to those of *Ctenacanthus*, *Antarctilamna*, and *Doliodus*, but is too poorly preserved for accurate determination. *Machaeracanthus* is the most widespread Devonian vertebrate in the Malvinokaffric Realm, and its spines are also known from the Old World and Eastern Americas realms, although scales referred to the genus are reported from outside these three regions. The occurrences of *Machaeracanthus* spines in the Parnaíba and Amazon basins lends support to an earlier proposal based on the distribution of invertebrate fossils that these basins provided maritime connections existed between the Malvinokaffric and the Old World/Eastern Americas realms during the late Eifelian - early Givetian.

Key words: Devonian. Pimenteira Formation. Parnaíba Basin. Malvinokaffric. Elasmobranch.

RESUMO: Alguns restos de peixes fósseis do Devoniano Médio (Eifeliano-Givetiano) da Formação Pimenteira da Bacia do Parnaíba, Nordeste do Brasil.

Restos de peixes fósseis do Devoniano Médio (Neo-eifeliano - Eogivetiano) são descritos da Formação Pimenteira, em sua faixa aflorante na margem oriental da Bacia do Parnaíba (região de Picos, PI, nordeste do Brasil). Os fósseis incluem um espinho de nadadeira ornamentado com costelas, um dente bicúspide de tubarão similar aos dos xenacantos e omalodôntidas, e um espinho mal preservado de *Machaeracanthus*. Além disso, registram-se pequenas escamas indeterminadas e possíveis fragmentos de cartilagem com calcificação prismática. O dente bicúspide constitui o primeiro achado dessa natureza no Devoniano do Brasil, sendo também o primeiro com registro inequívoco no Devoniano da América do Sul. Suas cúspides principais possuem cristas bem espaçadas entre si (tal como se verifica nos dentes de *Antarctilamna*, um elasmobrânquio devoniano do Gondwana), porém inexistem pequenas cúspides intermediárias (como em *Leonodus*). O espinho da nadadeira possui ornamentação comparável à de *Ctenacanthus*, *Antarctilamna* e *Doliodus*, porém a sua má preservacão não permite uma determinação segura. *Machaeracanthus* é o vertebrado devoniano com a mais ampla distribuição no Reino Malvinocáfrico, e seus espinhos são também conhecidos nos reinos do Velho Mundo e América Oriental, embora escamas referidas ao gênero tenham sido assinaladas fora dessas três regiões. A ocorrência de espinhos de *Machaeracanthus* nas bacias do Parnaíba e Amazonas reforça uma proposta anterior (baseada na distribuição de certos invertebrados fósseis) de conexões marinhas entre essas duas bacias e os reinos Malvinocáfrico, do Velho Mundo e da América Oriental durante o Neo-eifeliano - Eogivetiano.

Palavras-chave: Devoniano. Formação Pimenteira. Bacia do Parnaíba. Malvinocáfrico. Elasmobrânquio.

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INTRODUCTION

Reports of Devonian vertebrates are still rare in Brazil, so the presence of fossil fish remains in the Pimenteira Formation of the Parnaíba Basin (Maranhão Basin in earlier Brazilian literature) is therefore of considerable interest. CASTER (1948, 1952) first reported the occurrence of "fishbones" and "fish spines" in sandstones and "pebbles" (ferruginous concretions) of the Picos area, in State of Piauí, northeast Brazil. KEGEL (1953) and SANTOS (1961) also recorded spines attributed to *Ctenacanthus* Agassiz, 1835, *Machaeracanthus* Newberry, 1857 and *Devoncanthus* (now a *nomen nudum*) in the Picos region although no actual specimens were described. The material came from what was then termed the Picos Member of the Pimenteira Formation (see also CAMPOS, 1964; RICHTER, 1983). Subsequently, MELO (1988) mentioned that *Ctenacanthus* spines occur in the Pimenteira Formation, and a fin spine of "*Ctenacanthus* type" was later described by JANVIER & MELO (1992, fig.6). In addition to these Pimenteira occurrences, fragmentary fish remains of unknown affinity have also been reported by KEGEL (1953) from the underlying Itaim Formation, a Devonian rock unit originally defined as a lower member of the Pimenteira Formation (KEGEL, 1953; see also CAPUTO, 1984 and GÓES & FEIJÓ, 1994 for details about the regional Devonian lithostratigraphy).

The Pimenteira Formation (SMALL, 1914) consists of interlayered sandstones and siltstones/shales which were mostly deposited as tempestites (offshore bars or shallow shelf sediments with large-scale hummocky cross-stratification; DELLA FAVERA, 1982, 1990), which formed under the influence of storm-generated waves and currents. The base of the Pimenteira Formation marks the first widespread Devonian transgression across the Parnaíba Basin and conformably overlies the Itaim Formation, which has a much sandier character and is probably of fluvial to deltaic and shallow marine origin (CAROZZI *et al.*, 1975; CAPUTO, 1984). Both units were initially regarded as Early Devonian on the basis of megafossil evidence (CASTER, 1948; KEGEL, 1953; SANTOS, 1961), but subsequent palynological investigations suggest that the Pimenteira Formation is actually of Middle to Late Devonian age (DAEMON, 1974, 1976; ANDRADE & DAEMON, 1974). Acccording to the most recent miospore- and chitinozoan-based revisions, the bulk of the Itaim Formation is late Emsian to early Eifelian, whereas the Pimenteira Formation ranges in age from late Eifelian to late Frasnian or earliest Famennian (LOBOZIAK *et al.*, 1992, 1993, 1994a-b; LOBOZIAK & MELO, 2000, 2002; LOBOZIAK *et al.*, 2000; GRAHN, LOBOZIAK & MELO, 2001). However, due to a remarkable shift of lithofacies from west to east across the Parnaíba Basin, the Late Devonian part of the Pimenteira Formation is unknown in outcrops on the eastern side of the basin, where it is replaced by partly coeval sandstones of the overlying Cabeças Formation (CAPUTO, 1984; LOBOZIAK *et al.*, 2000). The older Pimenteira section (from which the fossil fish remains were recovered) crops out along both margins of the basin and is now considered to be entirely of late Eifelian - early Givetian age, placing it firmly within the younger end of the total time range of the Malvinokaffric Realm. Invertebrate fossils from the lower Pimenteira Formation (first recorded by CASTER, 1948 and KEGEL, 1953) have not been thoroughly investigated, but include a mixture of Malvinokaffric, Old World, and Eastern Americas elements, much like contemporary Amazon Basin assemblages farther to the west. For example, Malvinokaffric trilobites such as *Metacryphaeus* Reed, 1907 and *Burmeisteria* Salter, 1865, are present in the Pimenteira Formation (CARVALHO, EDGECOMBE & LIEBERMAN, 1997) although many other invertebrate taxa usually found in Malvinokaffric assemblages have not been recorded (MELO, 1988), and the Old World brachiopod *Tropidoleptus* Hall, 1857 also occurs here (FONSECA & MELO, 1991).

The fossil fish remains described herein, together with mudballs and indeterminate bivalves, occur as lag deposits within the basal, coarser-grained part of a fairly thick, hummocky cross-stratified, fining-upward sandstone bed that grades into overlying pelites with wavy/linsen structures (tempestites). A good exposure of these superposed tempestite units was found at a roadcut near the km 316 milepost of highway BR-316, about 5 km east of Picos city, State of Piauí, on the eastern border of the Parnaíba Basin (Fig.1). Stratigraphically, this section is well below the concretionary interval that yielded JANVIER & MELO's (1992) ctenacanthid spine, but is apparently higher than the basal Pimenteira position (F1-A in text-fig. 5 of JANVIER & MELO, 1992) from which *Ctenacanthus* and *Machaeracanthus* were reported east of Picos by KEGEL (1953) and SANTOS (1961).

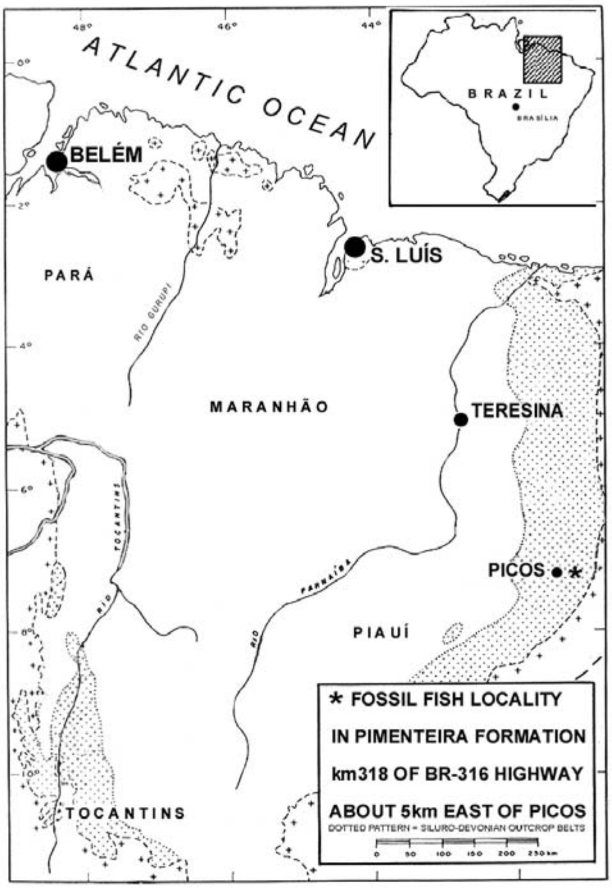

Fig.1- Map showing the locality in the Pimenteira Formation where the material was found.

The fish remains described here were originally associated in a single piece of matrix collected from the lower Pimenteira Formation in August 1991 by J.H.G.Melo, although they have now been separated for preparation and study. All the material is deposited in the Museu Paraense Emílio Goeldi, Belém, Brazil (MPEG 220-V). The remains are preserved in a coarse micaceous sandstone, mostly as natural casts, but microscopic fish scales are preserved within small rounded clasts (possibly the remains of coprolites) in the sandstone. Although the material fragmentary and not well preserved, it includes a *Machaeracanthus* spine and therefore confirms the presence of this form in the Pimenteira Formation. Another *Ctenacanthus*-like spine is also represented, as well as the external mold of a bicuspid xenacanth-like tooth, numerous microscopic scales and fragments of what may be prismatically calcified cartilage. This new sample therefore expands the record of marine fishes from the Pimenteira Formation and improves our resolution of the ichthyofauna in this part of western Gondwana during the Middle Devonian.

DESCRIPTION

CHONDRICHTHYAN FIN SPINE

The fin spine (MPEG 220-V-a) is approximately 95mm long, slightly recurved posteriorly, and seems to be bilaterally symmetrical (Fig.2). It is ornamented with numerous closely-spaced, narrow costae (ridges) extending over the lateral and anterior surface. The costae are not well preserved and it is uncertain whether they were originally ornamented with pectinations. The posterior wall of the spine is flat or slightly concave and lacks a median ridge distally. Such a ridge is present in fin spines of *Ctenacanthus sensu* MAISEY (1981). The posterolateral margins of the fin spine bear a series of approximately 15 small but distinct retrorse denticles, each one about twice as long as deep. The level of posterior closure has not been determined in the Pimenteira fin spine because its base is incomplete and there is little evidence of a posterior opening. Although the laterally-compressed shape and general arrangement of the ornament in the Pimenteira fin spine resembles that of many Paleozoic ctenacanth sharks, it is not possible to identify this spine to genus (see discussion below). The "*Ctenacanthus* type" fin spine from the Pimenteira Formation described by JANVIER & MELO (1992) also has pectinate ornament and may represent the same taxon as the spine described here. The identification of most isolated Paleozoic fish fin spines is problematic, especially those which were formerly referred to the form-genus *Ctenacanthus*. There is no convincing morphological evidence that "ctenacanth" sharks form a monophyletic group (MAISEY, 1981, 1982, 1984), or even how to characterize them, since sharks classified as ctenacanths share only plesiomorphic features (e.g., two dorsal fins, dorsal fin spines, "cladodont" teeth, anal fin) that are also found in many other extinct sharks. At best, "ctenacanths" can only be loosely defined on a phenetic basis, as extinct sharks that possessed "cladodont" teeth (discussed below) plus dorsal fin spines; some "cladodont"-toothed sharks lacked fin spines (e.g., symmoriids), and many "non-cladodont" sharks have fin spines (*e.g.*, *Hybodus* Agassiz, 1837, *Squalus* Linnaeus, 1758), but only "ctenacanths" have both. Thus, "ctenacanths" are almost certainly a phenetically defined grade-group that has no reality in nature.

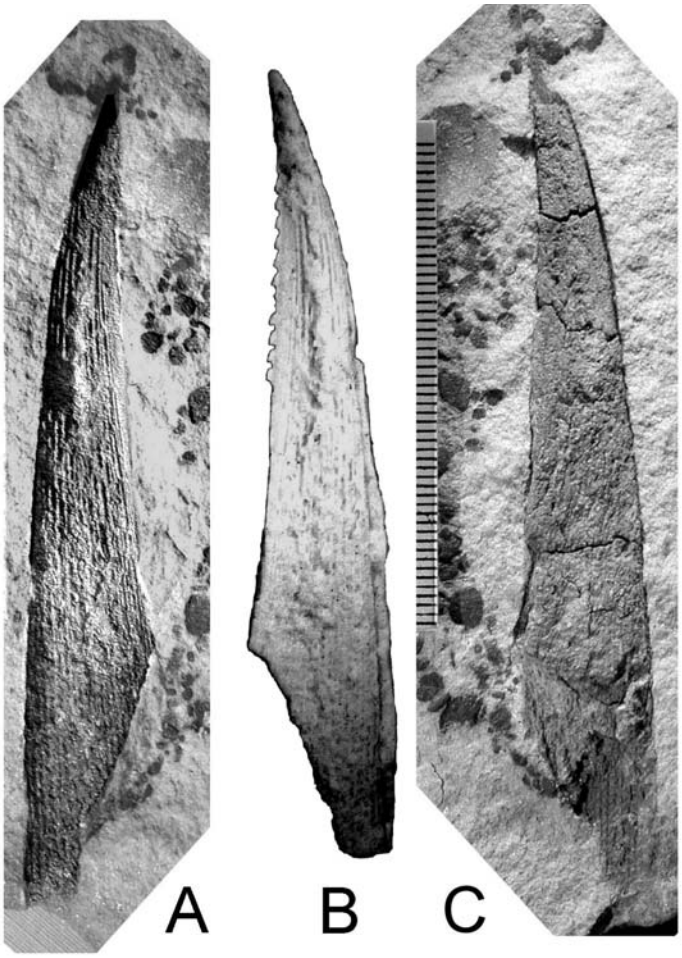

Fig.-2- Chondrichthyan dorsal fin spine (MPEG 220-V-a). (A), natural mold of spine; (B), silicone cast of spine prepared from natural mold, showing the right lateral surface; (C), counterpart of specimen with parts of spine still preserved. All views to same size; mm scale shown in (C).

Further complicating the picture, it has been suggested recently that paired pectoral fin spines were present in *Doliodus* Traquair, 1893 and perhaps in *Antarctilamna* Young, 1982 (MILLER, CLOUTIER & TURNER, 2001), although it is unclear whether these taxa had dorsal as well as pectoral fin spines. Originally it was thought that all chondrichthyan fin spines were unpaired and were inserted in front of the dorsal fins. Importantly, the ornament of *Antarctilamna* (and *Doliodus*) fin spines is remarkably similar to that of *Ctenacanthus* dorsal spines (*sensu* MAISEY, 1982). Although complete *Antarctilamna* and *Ctenacanthus* fin spines are distinguishable on the basis of morphological characters other than ornament, we can no longer assume that fragmentary *Ctenacanthus* fin spines are from the dorsal fin, or from sharks with “cladodont” teeth.

The Pimenteira fin spine displays few features of systematic value apart from its ribbed and possibly pectinate ornament pattern, the posterolateral denticle series, and the flat or concave posterior wall. Pectinate ornament occurs in another fragmentary fin spine from the Pimenteira Formation (JANVIER & MELO, 1992) and both specimens could belong to the same taxon. Posterolateral denticle rows like those observed on the Pimenteira specimen commonly occur in Paleozoic shark fin spines. In *Ctenacanthus*, these denticles are small, but in *Doliodus* they are comparatively large (WOODWARD, 1891). Fin spines referred to *Antarctilamna* lack posterolateral denticle rows (YOUNG, 1982). Unfortunately, the posterior wall is not preserved in the example described by JANVIER & MELO (1992) and it is unknown whether posterolateral denticles were originally present. The posterior wall of *Ctenacanthus* fin spines (*sensu* MAISEY, 1981) have a central ridge running along the posterior midline, gradually becoming obsolete proximally (although it is sometimes exaggerated by post-mortem crushing). A strong median ridge is present in hybodont fin spines (*e.g.*, *Hybodus*, *Asteracanthus*) Agassiz, 1837 and a weak ridge is present in *Antarctilamna*. The shape of this region has yet to be determined in *Doliodus* spines. In modern sharks (*e.g.*, *Squalus*, *Heterodontus* Blainville, 1816), the fin spine posterior wall is either flat or gently concave. While the shape of the spine posterior wall may have some systematic significance, its original shape is sometimes difficult to determine because this part of the spine is relatively weak and frequently collapses outward during fossilization, giving the appearance of a posterior ridge even where one may not have been present in life.

The length of the unornamented basal region and the angle of spine insertion are other important variables. *Antarctilamna* fin spines have a very short inserted region and a large basal opening which extends a considerable distance up the posterior wall (YOUNG, 1982), showing that the fin spine was not deeply inserted into the dorsal midline. It is unclear whether *Doliodus* spines had a deep insertion. Typical *Ctenacanthus* dorsal fin spines possess a long basal region which was deeply inserted at the dorsal midline (the “phalacanthous” arrangement *sensu* ZANGERL, 1973), and it is not uncommon for the anterior fin spine to be inserted more obliquely than the posterior one. Unfortunately, the inserted parts are not preserved in spine described here nor in the specimen described by JANVIER & MELO (1992). It is therefore uncertain whether these spines originated in the median or paired fins.

BICUSPID SHARK TOOTH

The bicuspid tooth from the Pimenteira Formation is the first such Devonian record from Brazil and is apparently only the second example reported from South America (the first is a poorly preserved tooth from the Upper Devonian of Colombia, tentatively referred to *Antarctilamna*; JANVIER & VILLARROEL, 2000). The slab containing the fin spine also includes the external mold of a single bicuspid tooth (MPEG 220-V-b), from which a latex peel was prepared (Fig. 3). Two principal cusps are present, both of which are slightly curved and divergent apically, as in xenacanths, *Doliodus*, and *Antarctilamna*. One cusp (approximately 6.5 mm tall) is exposed on the surface of the slab. The other cusp extends into the matrix but the latex peel shows it to be slightly shorter or almost equal in size to the exposed one. Using the terminology of xenacanth teeth proposed by JOHNSON (1999), the buried cusp is probably the major principal cusp, and the exposed one is the minor principal cusp. There is no evidence of any short intermediate cusps between the two principal ones. There is a medial cutting edge on both principal cusps, and a second continuous crista or ridge on the labial surface of each cusp, but no evidence of serrations along the cutting edges. The tooth base is not preserved, and it is therefore uncertain whether an apical button or basal tubercle was originally present.

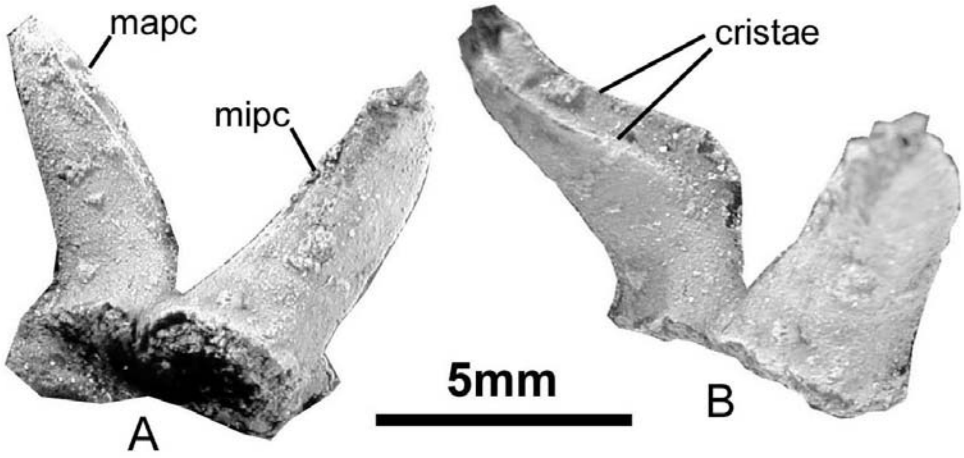

Fig.3- Diplodont tooth crown (MPEG 220-V-b). Two views of latex cast prepared from natural mold. (A), lingual view; (B), dorso-lingual view to show paired cristae. Abbreviations: mapc; major principal cusp; mipc, minor principal cusp.

Xenacanth teeth are characteristically bicuspid, with strongly divergent and asymmetrical principal cusps usually separated by one or more intermediate cusps, and with an apical button and basal tubercle on the basal plate (*e.g.*, *Diplodoselache* Dick, 1981, *Orthacanthus* Agassiz, 1843, *Triodus* Jordan, 1849). However, similar bicuspid tooth morphology is also characteristic of the earliest fossil shark teeth (*e.g.*, *Leonodus* Mader, 1986; Lower Gedinnian; MADER, 1986; *Doliodus*, Pragian/Emsian; MILLER *et al.*, 2001) and may represent a plesiomorphic gestalt for shark teeth. These early bicuspid teeth display considerable variation in presence or absence of an intermediate cusp, apical button, and basal tubercle, and in the extent to which the principal cusps are connected basally. Although xenacanths have bicuspid teeth, not all bicuspid teeth necessarily belong to xenacanths (many of the earliest forms with a labially extended base have been classified together within the Omalodontida; TURNER, 1997). Multicuspid “cladodont” teeth appear much later in the fossil record than bicuspid ones, lending biostratigraphic support to the notion that the latter are more primitive (supposed pre-Givetian “cladodont” records are considered unreliable; M. Ginter, pers. commun., 2002).

In xenacanths, intermediate cusps are sometimes absent (e.g., in some *Orthacanthus* and *Dicentrodus* Traquair, 1888 teeth; JOHNSON, 1999: HAMPE, 2003). In *Leonodus*, the principal cusps are widely separated and ornamented with cristae, an intermediate cusp is absent, and an elongated basal tubercle is present. YOUNG’s (1982) elasmobranch material from the Aztec Sandstone of Antarctica (late Givetian- early Frasnian) was referred to two genera; *Antarctilamna* teeth were characterized as bicuspid, with widely-spaced cristae on the principal cusps (resembling the Pimenteira tooth) but have one or two intermediate cusps between the principal ones; the other teeth (which he referred to *Xenacanthus* sp. Beyrich, 1848) lack both cristae and intermediate cusps. All the teeth described by YOUNG (1982) seem to lack an apical button and basal tubercle like those of xenacanths, and the two principal cusps in most of the teeth are separate or only weakly connected basally, instead of being broadly connected as in xenacanths. Thus, the Pimenteira tooth shows general similarities with both *Leonodus* and *Antarctilamna*, but cannot be referred with confidence to either genus.

Machaeracanthus spine

The *Machaeracanthus* spine (MPEG 220-V-c; Fig.4) is badly preserved, but its observed features (e.g., smooth surface, with a characteristic cross-section and bladelike keel) are characteristic of *Machaeracanthus* spines generally (although it is not possible to assign the specimen to any particular nominal species). *Machaeracanthus* spines are distinct from other chondrichthyan and acanthodian spines both morphologically and histologically. A pair of spines associated with perichondrally ossified scapulocoracoids and other skeletal elements was described by ZIDEK (1975). *Machaeracanthus* spines are always asymmetrical and it is possible that median ones were absent.

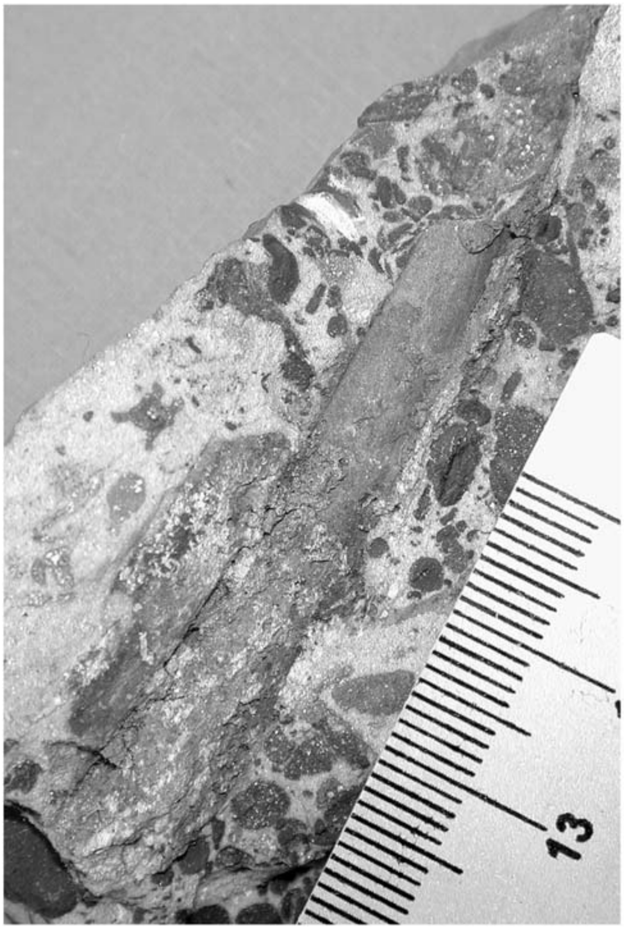

Fig.4- Badly preserved spine of *Machaeracanthus* (MPEG 220-V-c). Scale in mm.

Some specimens have been found associated with ischnacanthid-like tooth whorls and/or acanthodian scales (ZIDEK, 1975, 1981; MAISEY, BORGHI & CARVALHO, 2002), and *Machaeracanthus* is generally considered to be some kind of ischnacanthid acanthodian although its systematic position is still poorly resolved. Whatever its relationships, however, *Machaeracanthus* is the most widespread vertebrate known from the Malvinokaffric Realm.

The genus *Machaeracanthus* was originally founded on isolated spines and the type species (*M. peracutus* Newberry, 1857), has been documented from the Middle Devonian of Ohio, New York and Ontario, and from the Upper Emsian of Morocco (NEWBERRY, 1857; LEHMAN, 1976, 1977; DENISON, 1979; DINELEY & LOEFFLER, 1993). Malvinokaffric records encompass a wide geographic area including parts of Brazil (e.g., Pimenteira Formation, Parnaíba Basin; CAMPOS, 1964; RICHTER, 1983; LELIÈVRE, JANVIER & BLIECK, 1993), Antarctica (Horlick and Ellsworth Mountains; YOUNG, 1986; WEBERS *et al.*, 1992), South Africa (Lower Bokkeveld Group; ANDERSON *et al.*, 1999), Bolivia and the Falkland Islands (MAISEY *et al.*, 2002). There is also one further Brazilian *Machaeracanthus* record of note in the Amazon Basin, from the uppermost part of the Lontra Member of the Maecuru Formation (KATZER, 1897; MELO, 1988), an interval of proven Eifelian age that is correlative with the uppermost Itaim/basal Pimenteira interval of the Parnaíba Basin, according to recent palynological data (LOBOZIAK & MELO, 2000, 2002; MELO & LOBOZIAK, 2001, 2003). Like the Parnaíba Basin, the Amazon Basin has yielded a "mixed" invertebrate assemblage (including Malvinokaffric and Eastern Americas/Old World taxa), and is considered to be a biogeographic boundary area with a postulated Emsian-Eifelian marine connection to Bolivia or southern Peru (MELO, 1988).

There are many references in the literature to occurrences of Lower and Middle Devonian *Machaeracanthus* in other parts of the world, including New Zealand, eastern Australia, and China (MACADIE, 1985; TURNER, 1993; WANG, 1993; BURROW, 2000). However, no *Machaeracanthus* spines have been reported from those regions and the records are based solely on scales similar to examples found with *Machaeracanthus* spines elsewhere. Thus, the distribution of *Machaeracanthus* spines within the Malvinokaffric, Old World, and Eastern Americas realms (the maritime equivalent of the Euramerican province in YOUNG, 1981) is far more restricted than records of its scales. It is possible that the scales have simply been misidentified or that spines are under-represented in some parts of the world because of sampling or preservational factors, but it is also conceivable is that close relatives of *Machaeracanthus* lacked fin spines (especially since *Machaeracanthus* itself may have lacked median ones).

It is curious that there is strong endemism among invertebrates in the Malvinokaffric, Old World, and Eastern Americas realms, with only localized faunal mixing between the southern Malvinokaffric Realm and the northern Old World and Eastern Americas realms, yet *Machaeracanthus* spines occur in all three areas and apparently nowhere else. If this fossil record accurately reflects an original biogeographic distribution pattern, it is possible that the physical and/or physiological factors leading to endemism among invertebrates within these realms did not affect *Machaeracanthus*, whereas barriers to dispersal outside this larger region affected all these forms.

OTHER REMAINS

Other vertebrate remains include small patches of prismatically mineralized tissue (possibly parts of a chondrichthyan endoskeleton), and microscopic fish scales within phosphatic pellets (presumed to be coprolites or enteroliths). The size of the phosphatic pellets (if they are correctly identified) suggests the presence of a fairly large vertebrate predator (possibly the chondrichthyan), which was presumably feeding on much smaller prey.

DISCUSSION

All the vertebrate material described from the Pimenteira Formation is fragmentary and poorly preserved (like other Devonian vertebrate remains known from Brazil), but it nevertheless indicates that a diverse ichthyofauna including chondrichthyans, acanthodians, and perhaps osteichthyans was originally present. This material provides the basis for some interesting speculation about their taxonomic representation, diversity, and biogeographical significance.

Given that all these disarticulated remains were found together in the Pimenteira Formation, it is possible that some may belong to the same taxon (e.g., the fin spine and tooth, since bicuspid teeth and pectinate fin spines occur in the Devonian chondrichthyans *Antarctilamna* and *Doliodus*. GOUJET (1993) has suggested that *Leonodus* (founded on bicuspid teeth) may be congeneric with *Machaeracanthus* and JANVIER (1996, fig. 4.63E) even figured a *Leonodus* tooth under the name of *Machaeracanthus*. The Pimenteira tooth certainly resembles those of *Leonodus* in lacking an intermediate cusp, but the case for associating it with *Machaeracanthus* seems tenuous at best. The tooth and the pectinate fin spine could both be from a single taxon allied to *Antarctilamna*, although this also seems unlikely because the tooth lacks intermediate cusps and the fin spine has an elongated inserted basal region. It is unlikely that paired *Machaeracanthus* spines belong to the same taxon as the pectinate spine, because shark and acanthodian fin spines typically have similar morphological features and ornament whatever their position on the body. Well preserved endoskeletal remains of primitive chondrichthyan fishes have been described from Early and Middle Devonian Malvinokaffric localities in Bolivia and South Africa (e.g., *Pucapampella* Janvier & Suarez-Riglos, 1986, *Zamponiopteron* Janvier & Suarez-Riglos, 1986; ANDERSON *et al.*, 1999; MAISEY, 2001; MAISEY & ANDERSON, 2001), but none of the Pimenteira material can be referred to those taxa on the basis of available evidence.

No placoderm remains have so far been recognized from the Pimenteira Formation, nor from any other Devonian strata in Brazil. Although placoderm fishes were abundant and widespread in many parts of the world during the Middle Devonian, their remains are rare in Malvinokaffric localities of Emsian-Eifelian age. The rhenanid *Bolivosteus* Goujet, Janvier & Suarez-Riglos, 1986 occurs in Bolivia (GOUJET, JANVIER & SUAREZ-RIGLOS, 1985) and was probably endemic to part if not all the Malvinokaffric Realm (it has not yet been found at other localities). The only other Malvinokaffric placoderm remains that have been documented are some undetermined antiarch-like plates from the Lower Bokkeveld beds of South Africa (ANDERSON *et al.*, 1999).

CONCLUSIONS

1. Fossil fish remains from Middle Devonian strata of the Pimenteira Formation of the Parnaíba Basin include bicuspid chondrichthyan teeth, fin spines with *Ctenacanthus*-like ornament, *Machaeracanthus* fin spines, and possibly osteichthyan scales. The present findings thus corroborate JANVIER & MELO's (1992) observations and also confirm the previously unsubstantiated reports of *Machaeracanthus* in KEGEL (1953) and SANTOS (1961).
2. This is the first Devonian record of a bicuspid shark tooth from Brazil and is only the second such record from South America. The tooth may belong to a xenacanth shark, although the earliest recognizable shark teeth are also bicuspid and it could represent a primitive elasmobranch morphotype. The tooth differs from those of *Antarctilamna* and resembles *Leonodus* in lacking intermediate cusps. It cannot be assigned either to xenacanths or to omalodontids.
3. The fin spine has pectinate "ctenacanth" ornament but may not belong to *Ctenacanthus*. Unfortunately it is too poorly preserved for accurate identification. The spine differs from those described from *Antarctilamna* in having a flat or concave posterior wall and posterolateral denticles.
4. The presence of *Machaeracanthus* spines in the Pimenteira Formation suggests a marine connection between the Old World-Eastern Americas realms and

the Malvinokaffric Realm. No satisfactory explanation can be provided for the fact that the records of *Machaeracanthus* based on spines and scales worldwide are strongly discordant geographically.

5. Apart from the fact that all the material described here was contained originally in a single lithological hand sample from the Pimenteira Formation, only circumstantial arguments can be made for associating these remains (e.g., the unproven notion that *Leonodus* teeth and *Machaeracanthus* spines are from the same taxon, or the presence of bicuspid teeth and pectinate fin spines in *Antarctilamna*).

6. There is no evidence of endemic Malvinokaffric fishes such as *Pucapampella*, *Zamponiopteron*, or *Bolivosteus* in the Pimenteira Formation.

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